

ORIENTATION AND MOVEMENT OF WOLF SPIDERS *PARDOSA LAPIDICINA* (ARANEAE, LYCOSIDAE) IN THE INTERTIDAL ZONE

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ABSTRACT. Wolf spiders, *Pardosa lapidicina* Emerton 1885, occupy cobble beaches along the tide line about Narragansett Bay, Rhode Island, USA, and move back and forth on the beaches with the tides. I compared the orientation and movement in the low intertidal of three groups with normal access to the entire intertidal zone and a group from the high intertidal prevented from using the low intertidal by a barrier of dense salt-marsh cordgrass *Spartina alterniflora*. They included a group captured in the high intertidal (High), one captured in the low intertidal (Low), one from the low intertidal but not captured (Observed), and one captured behind cordgrass (Cordgrass). The High group moved farther and more unidirectionally than the others, and the Cordgrass group exhibited the most variable orientation of the manipulated spiders. All groups exhibited a roughly southwesterly orientation from the release site. The Low and Observed groups moved shorter distances than the others, and High individuals appeared more strongly inclined to leave the low intertidal than individuals initially positioned there (Low, Observed). Thus, experience likely played a role in the orientation and movement of the spiders.

Keywords: Circular statistics, cobble beach, experience, migration

Highly mobile animals exercise the option of moving about in their habitat to exploit scattered or periodically available resources. This mobility may provide special opportunities that give them an advantage over more sedentary forms. Wolf spiders, *Pardosa lapidicina* Emerton 1885, (Lycosidae) in the vicinity of Narragansett Bay, RI, exhibit the unusual, and possibly novel, habit of moving up and down the intertidal zone with the tides to forage in the intertidal (Morse 1997). Their behavior is thus a mirror image of the much better known aquatic species (fish, crabs, etc.) that move up into the intertidal to forage as the water level rises (Palmer 1995). Perhaps *P. lapidicina*'s closest parallel occurs in some high intertidal amphipods (Talitridae), which orient in response to several cues (e.g., Pardi and Papi 1952; Ugolini et al. 1986; Borgioli et al. 1999).

Given the potentially unique nature of *P. lapidicina*'s movements, it is of interest to inquire what factors govern them and their relationship to behavioral patterns found among spiders and other arthropods. Earlier I demonstrated that *P. lapidicina* hunting in the low intertidal capture significantly more prey than do those in the supratidal area (Morse 1997).

However, this difference does not account for how individuals perform their periodic migratory behavior. In this study I commence to address this question. Members of this population may provide useful insights into this question because they can be divided into subgroups that exhibit different movement patterns. On any given day, some individuals migrate down open cobble beaches to the low-tide line and others remain above the high-tide line at the same time. Censuses with marked individuals have demonstrated that some members of the latter group move down into the intertidal on subsequent days, although it remains unclear whether each one of them will do so at one time or another (Morse 1997). Other members of the population occupy adjacent stretches of the upper part of the cobble beach behind stands of salt-marsh cordgrass *Spartina alterniflora* that blanket a substantial part of the mid-zone region of cobble beaches in Narragansett Bay and prevent the spiders from moving down into the low intertidal. These cordgrass-confined individuals thus do not venture into the low intertidal during the summer and autumn of their first year, though they move over cordgrass stubble in the spring before the plants grow back to block their way (Morse 1997).

Releasing members of these different subgroups of spiders into the low intertidal during the early autumn should provide insight into how they develop and retain their ability to move up and down the tide line. Comparison of those captured in the low and high intertidal should permit separation of any motivational factors to commence movement, and comparison of these two with those isolated behind cordgrass permit evaluation of the role of experience in their performance. The individuals behind cordgrass are born in early summer and hence have had no opportunity to move to the low intertidal. Since one can compare all of these test individuals with undisturbed spiders in the low intertidal, it is further possible to control for any effects of handling.

Orientation is known in spiders, including lycosids (Papi 1955), though in a somewhat different context. Papi (1955) demonstrated that *Arctosa perita* (Latreille 1799), a widespread European species, could select the accustomed side of a stream when displaced, but only if the sky was not heavily overcast. When placed on the water away from the shore, individuals would seek the side from which they had been removed if the sky was clear; if heavily overcast, they would always seek the nearest banking. These spiders used a combination of sun-arc compass bearings, polarized light and local landmarks in orientation. Subsequently, Papi and others (e.g., Papi 1955; Tongiorgi 1959; Leech 1966) demonstrated that *A. perita* shared this trait with several other lycosids, and it has subsequently been discovered in additional spider families as well (Görner 1964). The results presented in this paper address the likely role of experience on a species that probably possesses these basic orientation capabilities common to many other lycosids and other spiders. This paper thus tests the hypotheses 1. that *P. lapidicina* exhibit orientation behavior in their migratory movements that is appropriate to the sites they occupy and 2. that experience enhances their performance at this task.

METHODS

Study animals.—*Pardosa lapidicina* is a small, darkly colored wolf spider of 6–9 mm length, with females somewhat larger than males. Over most of its range in eastern and central North America *P. lapidicina* occupies

rocky streambeds (Kaston 1948; Eason 1969). Its much more poorly known exploitation of intertidal and supratidal areas appears confined to cobble shores, the species thus far not being reported from ledges and sandy or muddy marine shorelines. This high degree of habitat specificity thereby generally limits its marine range to glaciated areas of the northeast, from Connecticut northward. In much of coastal Maine the appropriate cobbles currently lie below sea level, the consequence of a sinking coastline; however, small, dark *Pardosa* C. L. Koch 1848 occupy intertidal cobbles from Mt. Desert Is. (Hancock County) eastward (K. Fink, pers. comm.; S. Zimsen, pers. comm.).

Voucher specimens of *P. lapidicina* have been deposited in the National Museum of Natural History, Smithsonian Institution.

Study area.—I conducted this work at the Haffenreffer Estate of Brown University, Bristol, Bristol County, Rhode Island from August 1994–September 1999. The study area is a cobble beach of 40 m length located on the west shore of Mount Hope Bay, a partially sheltered eastern arm of Narragansett Bay. Tides average 1.4 m, and the mean width of the beach at low tide is 23 m. Most cobbles range from 10–30 cm in the experimental area, with some smooth smaller stones (3–8 cm in length) overlying them at the upper edge of the beach. Some bladder wrack seaweed *Fucus vesiculosus* and a variety of encrusting organisms grow on the larger cobbles.

The study area is bounded on both sides by similar beach that has been overgrown by cordgrass, which covers the middle ranges of the beach (10 m from the top of the beach to 5 m above the low-tide line). The grass is dense, with about 1400 stems/m² (Morse 1997), which prevents *P. lapidicina* behind it from gaining access to the low-tide area. The beach is bounded on its upper side by second-growth forest. The study area is described in further detail by Morse (1997), Bertness (1999:239–242), and Fig. 1.

Experiments.—I investigated the orientation of *P. lapidicina* with four groups of individuals, all tested during low tide in the lower intertidal zone, and referred to throughout as the High, Low, Observed, and Cordgrass groups. Sample sizes in all analyses are 30, 24, 40, and 22, respectively. Members of the

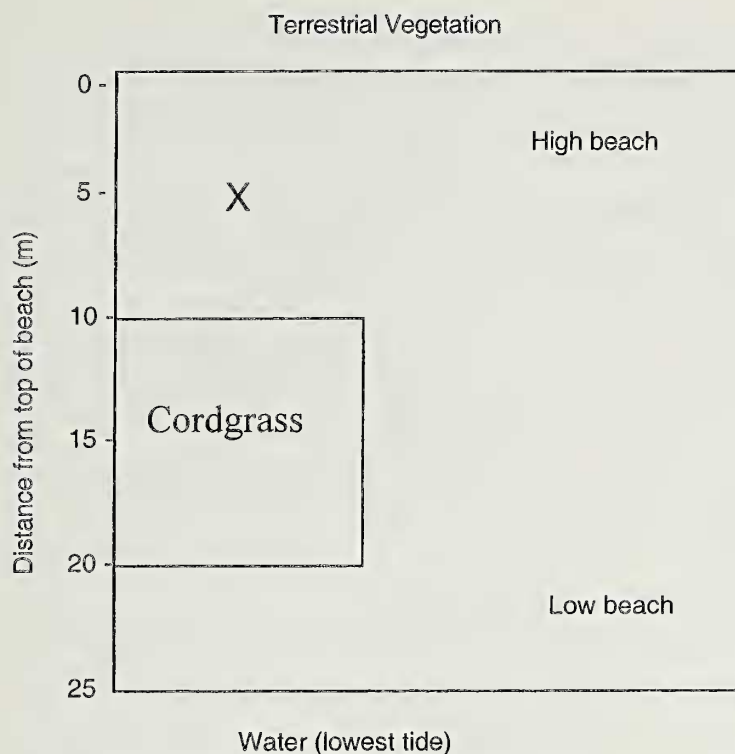


Figure 1.—Diagram of part of study site with both open beach and cordgrass *Spartina alterniflora* areas, as well as capture and release sites of spiders. Capture site of high intertidal group (High) in high-beach area; capture site of low intertidal group (Low) in low-beach area; capture site of group isolated behind cordgrass (Cordgrass) in area denoted by large X; site at which low intertidal, unhandled group observed (Observed) was also in low-beach area. All runs were made in low-beach area, to right of cordgrass in figure.

High group were collected above the high tide line within 5 m of the edge of the forest. They thus had not moved down the beach with the last tide, thereby separating them from individuals in the Low group. Members of the Low group did follow the last tide down into the low intertidal, where they were collected. Another group, the Observed group, also consisted of individuals that moved down the tide line into the low intertidal, where the performances of all the groups were studied. However, they were not collected or manipulated in any way. Lastly, the Cordgrass group was captured immediately above the cordgrass stand, which blocks access of these individuals from the low intertidal, both to the north and south of the beach.

Members of the High, Low, and Cordgrass groups were captured in large plastic containers (30 × 18 × 10 cm) placed on their side and partially sunken into the cobble so that the spiders could readily be driven into them. The spiders were then transferred to 7 dram plastic vials (5 cm tall, 3 cm diameter). All

individuals of the High and Cordgrass groups were captured within 20–40 m of the test site. I carried members of the four groups about the beach in their vials for periods and distances similar to those of the High and Cordgrass groups. Thus, I handled all three experimental groups as similarly as possible. They were then inverted on a flat stone 1–2 m from the water's edge. Care was taken not to release more than one individual at the same site on a given day, in order to eliminate the possibility that they might follow a line laid down by an earlier tested individual. The vials were left inverted for 2 min, to allow the spiders to acclimate, and then removed. The spiders were subsequently followed for 10 min, and the number, distance and orientation of their movements, as well as their overall displacement from the release site, recorded. We randomly shifted our observation site, as well as hand position in removing the inverted vial, between the north and south side of the release site in order to avoid the chance of systematically influencing the spiders' mean directional movement. Members of the Observed group were located in the low intertidal, and data on them gathered similarly to the other groups. Runs of these individuals commenced after they had come to a full stop.

For purposes of analysis, these data were broken into three observation periods (initial movement, < 2 min, 2–10 min), as well as analyzed as a whole (referred to as mean). Distances were measured with a meter stick, and directions estimated with aid of a clipboard sheet bearing compass orientations that could be quickly calibrated with the beach-forest interface, which lay immediately west of the shoreline. A move consisted of a continuous or nearly continuous directional motion, with instances in which individuals paused in the midst of a bout for no more than 1–2 sec treated as a single move. Moves, as thus defined, generally were interspersed by 15 sec to 2 min. Care was taken to remain 2 m or more from the spiders during this time, in order not to bias their activity. All tests were run under clear skies.

Circular statistics were employed to compare the direction of movements by the spiders. Details of the tests used, and their rationale, can be found in Batschelet (1981) and Zar (1999).

RESULTS

Orientation.—None of the groups (High, Low, Observed, Cordgrass) moved in random directions in any of the observation periods (initial, < 2 min, 2–10 min: Fig. 1; mean). Each measure of all four groups was highly significantly different from a von Mises distribution (circular equivalent to random distribution) at all four observation periods [total = 16 analyses; $Z = 10.21$ – 24.02 ; $N = 20$ – 40 , $P < 0.001$ in all instances: Rayleigh Z Test for circular uniformity (Zar 1999)]. Differences from random would be predicted for all but the initial movements, since the release sites of the experiments lay no more than 1–2 m from the water's edge, and most individuals moved considerably more than a total of 1–2 m in their collective runs. However, initial movements should not be subject to that constraint, since they usually did not approach 1–2 m in length, and they were commenced at the latter distance from the edge.

A natural prediction is that the spiders leaving the site would move directly up the beach; that is, due west (270°), perpendicular to the beach (Papi 1955). However, all of the groups differed significantly from 270° at each observation period [modified Rayleigh V Test for mean direction: Zar 1999 ($\mu = 4.18$ – 6.49 ; $N = 20$ – 40 , $P < 0.001$ in all instances)], in most instances exhibiting a roughly southwesterly direction. Nevertheless, their orientation during the 2–10 min period fell nearer to due west than at other periods (Fig. 2).

Initial moves of the High group differed in direction from those of the other three groups [Table 1: Watson U^2 tests (Zar 1999), with sequential Bonferroni corrections (Rice 1989)]; however, none of the other groups differed significantly among themselves at this stage (same tests). The High group differed from the others in making very few initial moves in a northerly direction, while the others' moves spread more broadly into that direction (Fig. 2). During the first 2 min, only the Observed group differed significantly from the others, largely as a result of retaining an extremely wide directionality of moves, while the other groups conspicuously narrowed their directionality, in that way resembling more closely the performance of the High group in their initial moves. Subsequently, the High group again diverged significantly from the others,

being more strongly directional than the others over the remainder of the observation period. The mean results closely followed those of the 2–10 min group.

Distance moved.—The four groups differed significantly in distance traveled from the original starting point (Fig. 3) ($H = 32.21$, $df = 3$, $N = 116$, $P < 0.001$, Kruskal-Wallis 1-way ANOVA), with most of the difference resulting from the High group moving considerably farther from the starting point than any of the other three groups. Analyzing only the first 2 min in an effort to determine whether initial responses differed among the groups (a possible handling effect) results generally resembled those for the entire 10-min period ($H = 25.76$, $P < 0.001$, same test), with the High group again moving considerably farther than the other groups, and the Cordgrass group moving farther than the Observed group. Data for min 2–10 closely followed those for both the entire 10-min period and the first two min ($H = 21.73$, $P < 0.001$, same test).

The measures reported thus far present total distance from the starting site and do not consider any extra distance resulting from backtracking or otherwise deviating from the eventual direction. Total distances, thus measured, also differed strikingly from random ($H = 43.12$, $P < 0.0001$, same test), generally resembling those of distance from the starting site (Fig. 3). However, the proportional differences between total distance moved and distance from starting point to ending point of a run, a measure of consistency of direction, varied significantly among the groups ($H = 7.82$, $P < 0.01$, same test). In particular, the Cordgrass group moved in much more variable directions than the other three groups (Fig. 4). Thus, though the High group did not move significantly more than the Cordgrass group, it moved significantly farther from the release site as a result of its much more consistent orientation.

Modest differences occurred in the number of moves made by the different groups (Fig. 5) ($H = 9.78$, $P < 0.02$, same test), with the High group somewhat greater than the other groups. Therefore, differences in total movement were primarily a consequence of the length, not frequency, of moves, although numbers of moves contributed somewhat to that disparity.

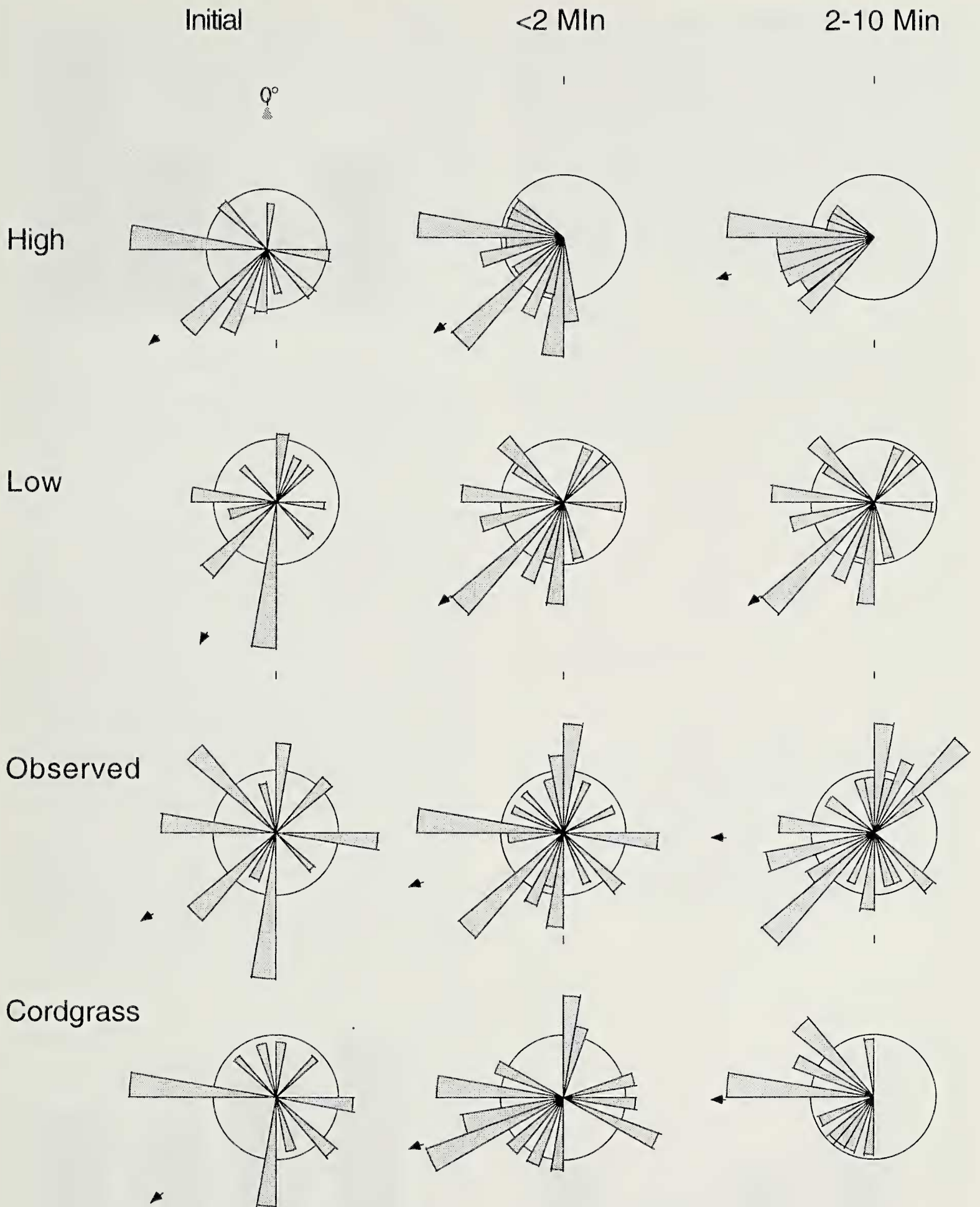


Figure 2.—Rose diagrams denoting directionality of movement during different parts of experimental runs by *Pardosa lapidicina* from the four sites. Mean over entire test period very similar to that of 2–10 min period and therefore not figured. Each wedge in a figure = 10°. Distance from center to periphery of circle = ca. 1.5 observations. Gray arrowhead in upper left figure points to 0° orientation (north). 0° orientation in other figures denoted by thin dash in same position. Black arrow = mean direction of movement of the 20–40 individuals at each stage. Due left = 270° (west), a trajectory taking spiders directly up the beach. Rose diagrams are circular histograms with wedges scaled to represent the relative proportions of measurements falling in each class interval (Zippi 1987–2000).

Table 1.—Differences in orientation among the four groups of spiders at different periods of their trials, presented as U^2 and significance levels. * = $P < 0.05$ in Watson U^2 tests (Zar 1999) with sequential Bonferroni corrections (Rice 1989), U^2 with no *: $P > 0.05$.

| PERIOD | GROUP | | |
|----------|-------|----------|-----------|
| Initial | Low | Observed | Cordgrass |
| High | .258* | .261* | .296* |
| Low | | .177 | .212 |
| Observed | | | .135 |
| <2 min | | | |
| High | .079 | .223 | .125 |
| Low | | .110 | .128 |
| Observed | | | .265* |
| 2–10 min | | | |
| High | .547* | .837* | .366* |
| Low | | .197 | .097 |
| Observed | | | .315* |
| Mean | | | |
| High | .381* | .643* | .141 |
| Low | | .304* | .089 |
| Observed | | | .274* |

DISCUSSION

Differences among groups.—Members of the different groups varied in several important ways. First, members of the High group differed markedly from the others in both their focused orientation and the maximum distance they moved away from the release site. They

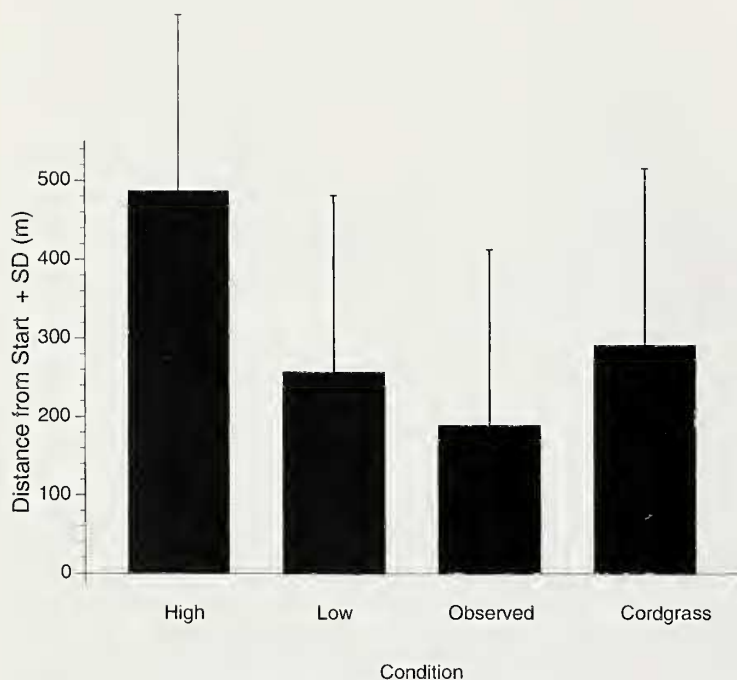


Figure 3.—Distance ($\bar{x} \pm SD$) moved by four groups of spiders ($\pm S.D.$) over 10 min period following release.

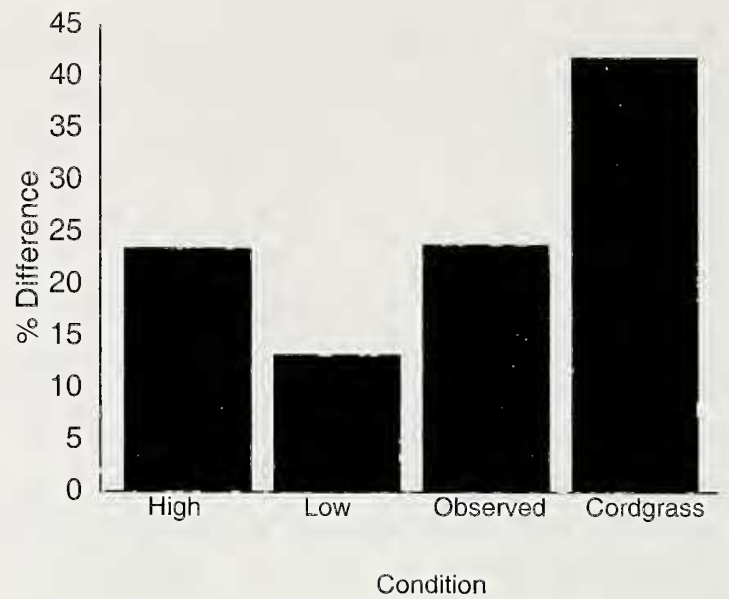


Figure 4.—Percent difference between total distance moved and distance from start by four groups of spiders over the 10 min period following release.

thus responded as if they were aware of their location and that it was unsatisfactory to them. This behavior is consistent with them being familiar with the intertidal area, even though they did not occupy it on the days they were tested. The demonstrably naïve Cordgrass individuals exhibited the most variable orientation of any of the three experimental groups (Fig. 4). Though moving so much that their total travel distance did not differ significantly from that of the High group, their straight-line distances differed significantly, because of their constant shift in orientation. Thus, although both groups appeared highly motivated to leave the release site, the High group's experience apparently permitted them to move away from it more effectively than the Cord-

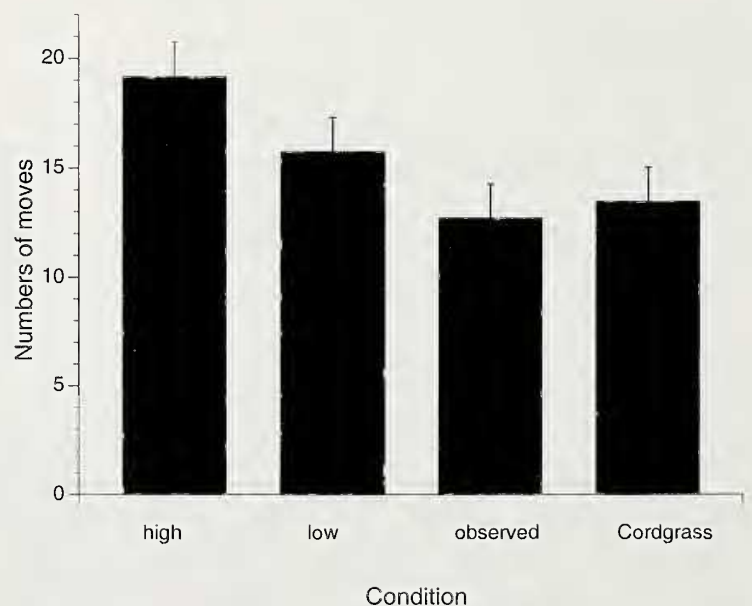


Figure 5.—Number of moves by four groups of spiders ($\pm S.D.$) over the 10 min period following release.

grass group. If so, then accurate movement up and down the tide line depends on learning from earlier experiences in the habitat, which the Cordgrass individuals lack. The shorter distances moved by the Low and Observed groups may reflect their being at or near sites they had just been occupying. The higher variation of direction by the Observed group may reflect a somewhat different motivational state from that of the other individuals, though their similarity of performance to the Low group reflects their perceived quality of the site. The results thus suggest that experience (and probably learning) plays a role in honing the exploitation patterns of the spiders. Spiders and other small invertebrates are known to be capable of learning responses to simple stimuli such as these (Morse 2000; Heinrich 1979; Vet & Papaj 1991).

Although one might question whether the differences reported between experienced and inexperienced individuals produce enough benefits to generate and maintain such behavior, the increase in proficiency likely translates into extra hunting time. It may also mediate risk encountered from being swept off the site by unanticipated waves (Morse 1997), which cast them into water containing large numbers of small predatory fish, primarily silversides *Menidia menidia* (pers. obs.). These spiders move formidable distances (> 40 m) during a single trip up and down the beach, and the differences in time required to execute these movements should suffice to enhance the value of such a difference. Such abilities are likely obtained during early instars, because the spiderlings begin to move extensively down the tide line by their third instar, in July (Morse 1997). I have no data on their orientation abilities at this time, but Papi and Tongiorgi (1963) reported that young *Arctosa perita*, a European lycosid, develop orientation abilities early in life.

These spiders capture significantly more prey in the low intertidal than they do above the tide line (Morse 1997). Hence, condition could account for the relatively low movement rates of both the Low and Observed groups, which occupied positions from which they might have captured prey immediately before we recorded their activity levels. Hunger affects the activity rates of some (Walker et al. 1999; Persons 1999), though not all (Provencher & Reichert 1991) spiders. If only

hungry spiders moved into the lower intertidal, as seems likely (Morse 1997), it is improbable that movement of the High group would significantly exceed those of the other groups, however. Further, light-bodied cursorial lycosid species [*Pardosa milvina* (Hentz 1844)] appear less likely to modify their activity rates in response to different levels of starvation than did heavy-bodied lycosids [*Hogna helluo* (Walckenaer 1837)] (Walker et al. 1999).

Orientation.—All four groups moved in a predominantly southwesterly to westerly direction over the course of the manipulations. This result could not have been a consequence of their collection sites, because roughly similar numbers of individuals taken for the High sample came from sites to the northwest, west, and southwest of the release area, and similar numbers from the Low samples came from sites to the north and south of the release area. Additionally, I randomly shifted the observation site, so that roughly half of the spiders were observed from the north side and half from the south side. Papi & Syrjämäki (1963) found that *Lycosa fluviatilis* (Blackwall 1861) [= *Pardosa agricola* (Thorell 1856)] from sites normally without access to the unbroken sky performed less consistently in orientation experiments than did individuals from adjacent barren areas that provided unobstructed views of the sky. The markedly greater variance in direction of the Cordgrass group is consistent with this factor as well as an unfamiliarity of the intertidal sites.

The only closely comparable information on orientation by displaced individuals I have found involves *Pardosa pullata* (Clerck 1757), a common species along European shores. *Pardosa pullata* exhibited a well developed pattern of orientation when displaced down the beach (Bristowe 1958). All members of a sample of 50, so displaced, moved up the beach, either immediately or by quickly angling around to an up-the-beach orientation, which they then adopted. Several of the *P. lapidicina* placed low in the intertidal similarly first moved toward the water before angling about and moving up the beach. In some instances the *P. lapidicina* reached the edge of the nearby water 1 m or more seaward of their release site before changing directions and moving up the beach. In his single test, Bristowe (1958) reported none of the variability

in performance that I found in samples of *P. lapidicina* taken from different sites, but his brief report contains so little detail that it is not possible to eliminate the possibility of such variance.

Other lycosids, including members of the genus *Pardosa*, are well known to exhibit orientation abilities (Papi 1955; Tongiorgi 1959; Leech 1966), which depend at least in part on the use of polarized light, in some instances known to be mediated through the anterior medial eyes (Papi 1955; Ortega-Escobar & Muñoz-Cuevas 1999). When placed in a strange environment with a polarized light source these spiders oriented in a direction that would normally return them to their site. For instance, if displaced from a shoreline site, they oriented and moved in the direction that would normally move them back to that shore (Papi 1955). If released under an overcast sky, however, they moved toward the closest object (Papi & Tongiorgi 1963), apparently using conventional visual stimuli under those circumstances. Although I did not test for the precise mechanism involved, the consistent tendency of all groups of *P. lapidicina* to move in a southwesterly direction, despite their differences in precision, is also consistent with these spiders using some form of astronomical cues in orientation.

Dondale & Redner (1990) report that both *P. labradorensis* (Thorell 1875) and *P. groenlandica* (Thorell 1872) frequent intertidal cobble and stony beaches of Atlantic Canada and Greenland. These species are likely candidates to exhibit behavior similar to that of the *P. lapidicina* described in this paper. Curiously, Dondale and Redner do not list intertidal cobble among the habitats frequented by *P. lapidicina*. The literature thus suggests that such behavior is uncommon among spiders in the intertidal area, but the habitat has been so poorly studied from this perspective (Morse 1997) that this conclusion must be regarded as provisional.

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